GEORGINIDAE, NEW FAMILY OF ACTINOCERATOID CEPHALOPODS, MIDDLE ORDOVICIAN, AUSTRALIA

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ABSTRACT

150 Actinoceratoid cephalopods from Lower Middle Ordovician rocks in Toko Syncline, Georgina Basin (NW. Queensland and E. Northern Territory) have siphuncular calcification in which not only does each annulus consist of a hollow ring of enveloping wall enclosing radially arranged lamellae but a series of more massive calcareous growths are formed on the inside of the connecting rings, and engrafted across the plane of contact of adjacent annuli (the interannulus) as they and the annuli grow. Both are formed of fine calcareous spicules normal to apparent membrane surfaces. The canal systems are closely comparable with those of normal Actinoceratida. This new family Georginidae comprises *Georgina* n.gen., *G. andersonorum* n.sp., *G. taylori* n.sp., *G. beuteli* n.sp., *G. linda* n.sp., *G. dwyeri* n.sp., *Mesaktoceras arachne* n. gen., n.sp. The last 3 occur in younger beds than the remainder, but only *G. beuteli* and *G. dwyeri* could evidence parts of an ancestor-descendant series.

In 1970 Mr D. J. Taylor of Sydney suggested to me that the collection and study of the Coolibah Formation nautiloids (which he had sampled in 1958) would be a rewarding project. He specified the two richest areas he had observed, one of which, Halfway Dam on Tobermory Station, was exceptional. Collecting trips made in 1971, 72, and 74 have amply justified his advice.

The Lower Palaeozoic Georgina Basin extends from NW. to SE. across the border of the Northern Territory of Australia and Queensland (Fig. 1a). To the SE., it is lost to sight beneath younger sediments of the Great Artesian Basin. Its main sediments are predominantly low dipping Cambrian and Ordovician rocks; known Silurian rocks are restricted to Toko Syncline (the most southerly. major structure exposed) and known Devonian rocks to a few synclines, one of which is Toko Syncline. The subject of this paper is part of the Ordovician nautiloid fauna of Coolibah and Nora Formations in Toko Syncline. The syncline takes its name from Toko Range which is formed by the NE. limb and axial plateau north of the fault zones near Burnt Well, Tobermory (Fig. 1c). Toomba Range is the SW. limb of the syncline. The scarps of the ranges are formed by Carlo Sandstone, conformably above Nora Formation which forms the lower part of the scarps (where it is often totally concealed by talus) and a varying width of surrounding flat land. Coolibah

Fm. embraces the ranges and may form a low secondary ridge. In Toomba Ra. extensive faulting and outwash deposits conceal it from just north of Gap Homestead to 4.8 km S. of Eurithethera Soak. At this spot (L326 on Fig. 1c) a tiny outcrop of its upper beds is sandwiched between Nora Fm. and a strike fault which brings light grey Ninmaroo Fm. limestone against similar upper Coolibah limestones. This is the only known outcrop of its upper beds in Toomba Range but the middle beds outcrop further S. because the fault is not quite parallel to the strike. Its southward extension is concealed N. of a series of en echalon transverse faults which displace the tip of Toomba Range. The presence of this unmapped strike fault may help to account for the report of a local fourfold increase in thickness of the Coolibah Fm. in this region (Reynolds 1968, an unspecified section).

Smith (1972) has summarized years of geological mapping by geologists of the Bureau of Mineral Resources, Geology and Geophysics aided, in Queensland, by the Queensland Geological Survey. The Bureau of Mineral Resources 1:500,000 geological map Georgina Basin sheet 4, compiled by Smith (1965b), was the base map used in Fig. 1c. In this map and in Smith (1972) the Lower to Middle Ordovician boundary is placed between Coolibah and Nora Fms. on unpublished palaeontologic evidence. This course was also followed in the 1:250,000 geological map series SF/54-9, 13,



FIG. 1a-c. Locality plan of Georgina Basin and Toko Syncline showing outcrop of Coolibah and Nora Fms, Lower Middle Ordovician, embracing Toko and Toomba Ranges. After Smith, 1972.

SF/53-12, and in the explanatory notes to accompany those sheets: Glenormiston, Mt Whelan (Reynolds 1965, 1968) and Tobermory (Smith 1965a). This placing is still under mainly verbal debate by workers on several fossil groups and cannot be regarded as final. Two *Armenoceras* sp. appear among the earliest nautiloids in Coolibah Fm., about one third of its thickness above its base, and of them one is long-ranging and reaches virtually to the top of the formation, being accompanied in the last one or two metres by two larger species of *Armenoceras*. These faunas are necessarily post-Canadian and, although new species, would appear to be quite high in the Whiterock (Flower 1968, fig. 1), were it not for the accompanying endocerids which have a low Whiterock aspect (Flower, pers. comm.). The entry of large *Armenoceras* in the highest Coolibah

beds is followed, in limestone lenses in the lower third of the Nora Fm., by a much richer fauna of still larger Armenoceratidae and the first Actinoceras. The endocerids however have an older aspect and it seems unlikely that these beds can be considered younger than Chazy (Flower, pers. comm.), so this numerous species is the oldest known Actinoceras. The nautiloids figured by Hill, Playford and Woods (1969) from Nora Fm. include three specimens mistakenly published as from Coolibah Fm. (Hill, Playford and Woods 1969, pl. OII, fig. 8 and pl. OIII, figs. 6, 7); they bear the original University of Queensland locality number L271 = 'base of low mesas S. of Wheelaman Bore' besides being unsilicified like the Nora fossils and unlike any rock-free Coolibah fossils. Both species of the U.Q. L271 specimens are found in a widespread lower Nora fauna richest at L319 in

Toomba Ra., while the remainder of Hill, Playford, and Woods' figured specimens are from another widespread lower upper Nora fauna. Published localities for all the latter agree with locality numbers on the specimens. The overall aspect of the nautiloids thus suggests that the age of the Coolibah and Nora Fms. ranges through the Whiterock to reach Chazy possibly before the end of Coolibah deposition but certainly by the lower Nora Fm. Many elements drop out well before the top of the Nora but the highest beds are decalcified and their dating is not discussed here as no Georginidae were recognized in them.

The Coolibah Fm. has repetitive, variable lithology and cannot be divided lithologically; though it can already be subdivided on actinoceratoids the formal establishment of zones should await study of other nautiloid groups. It has no nautiloids in its

occurences on SW.limb occurences on NE.limb TOKO SYNCLINE GEORGININA	Georgina taylori	Georgina andersonorum	Georgina beuteli	Georgina sp.	Georgina linda	Mesaktoceras arachne	Georgina dwyeri
Upper Nora							•
Middle Nora							
Lower Nora							
Upper Coolibah	•	• • • •?	• • • • • •				
Middle Coolibah							

FIG. 2. Stratigraphic distribution of Georginidae in the Middle Ordovician of Georgina Basin.

basal part, a fauna of endoceratoids, *Armenoceras* spp. discosorids, and a tarphycerid from one third of the way above the base, and an upper fauna which includes further species of *Armenoceras* and the new actinoceratoids described below as the new family Georginidae. On the NE. limb the lower fauna is the better developed while the upper fauna is the better on the SW. limb. The Georginidae enter at approximately the same level (Fig. 2). Also shown on this chart is a discontinuous series of occurrences in the conformably overlying Nora Fm.

The Nora Fm. is lithologically variable between sandstone and coquinite; when fresh it is strongly glauconitic, and phosphate nodules occur intermittently. Thicknesses vary greatly (Smith 1972) as does the proportion of carbonate. Nautiloids are confined to the beds with carbonate (or clearly decalcified beds now sandstone, forming the top of the formation). Georginidae occur in lenticular carbonates at three levels in the Nora. There is a supporting fauna of other nautiloids so that the sequence of forms shown in Fig. 2 is considered reliable even though large-scale lensing of beds makes nonsense of lithological subdivision without very detailed fieldwork. Reynolds (1965) discussed the Nora Fm. in terms of a 'basal' portion of fine sandstone to coquinites 120 feet [36 m] thick, and an overlying sequence of siltstone to sandstone 76 feet [23 m] thick. Abundant moulds in many layers testify to a laterally variable, high proportion of shell carbonate originally having been present in this upper portion. Nautiloid internal moulds are of endoceratoids and possible discosorids and actinoceratoids but no Georginidae are known. Generally in the syncline, these highest beds are somewhat transitional to the overlying Carlo Sandstone. Of the three divisions in Fig. 2, lower, middle, and the lower part of the upper division are all equivalent to Reynolds' 'basal' 120 feet [36 m], the blank upper part of the upper division is equivalent to Reynolds' 76 feet [23 m] siltstone to sandstone. This usage is based on the sequence at L319 on the E. side of Toomba Ra. scarp (where the base is concealed). There a large lens, estimated to be about 1/3 of the distance from bottom to top of the formation, contains the rich 'lower Nora' fauna (including 3 georginids, one undescribed because all specimens are worn). This fauna is known elsewhere from lenses at L251 near the observed base of the formation, and L327 (Fig. 1). At about 2/3 the distance from bottom to top of the formation near L319 a thin lens of limestone carries the 'middle Nora' fauna, endoceratoids and one of the three georginids (Mesaktoceras; a thicker lens in this position near Halfway Dam also

contains this georginid). An upper bed, not far below the sandy beds that grade into the overlying Carlo Sandstone, contains the fauna which accompanies the largest georginid known (as yet found only on the NE. limb), the 'lower upper Nora' fauna. This georginid occurs in the lower half of a major coquinite near the top of Reynolds' 'basal' bed. On the NE. limb the lower fauna is known only from an old collection of F. W. Whitehouse (Univ. Qd L271) and Qd Museum L251. The section is thinner, and phosphatic nodules are very generally larger and more common than on the SW. limb. Attenuation appears more likely to be due to repeated reworking than to a major disconformity; frequently specimens have been planed off after burial and later re-buried by sediment. Some have been planed off more than once.

DEPOSITORIES

Most holotype and paratype material is deposited at the Queensland Museum, register numbers F7090 to F7212, F7219 to F7221. The remainder of the material is deposited at the Geology Department, University of Queensland, register nos. F66033, F60014 and F67153, and Bureau of Mineral Resources, Geology and Geophysics. Canberra, A.C.T., register no. CPC16908.

SYSTEMATICS

MORPHOLOGY OF THE GEORGINIDAE

The new family Georginidae had orthoconic shells with relatively long chambers. Only two partial phragmacones have been collected and both are of thin-walled shells without cameral deposits, though enclosing fully developed, calcified siphuncles. There are no other indications of cameral deposits. The destruction of shells speaks for their delicacy, as does the fact that septal necks and adjacent pieces of septa are very fragile for the sizes of shells indicated by the siphuncle fillings. Most of the specific descriptions are necessarily based on the siphuncular deposits which consist, as in other Actinoceratida, of calcified annuli extending from the septal necks outward along the connecting ring until they impinge on the annuli anteriorly and posteriorly, and inwards to surround an axial space a little larger than the axial canals. The interannuli (the contact areas, or zones, between adjacent annuli) are not necessarily flat but have a characteristic range of shapes in any species, frequently becoming anteriorly projected near the centre as the individual matures and septa become more closely spaced. Plate 1, fig. 5 shows the only



FIG. 3. Georgina taylori n. gen., n. sp. approx. $\times 2$ and $\times 6$. Diagram showing relation of annulus calcification normal to its basal membranes (wall membranes and radial lamellar membranes); double-walled nature of interannulus (heavy black line) and insertion of engrafts between the edges of adjacent annuli.

remains which indicate shell shape, in oblique longitudinal section.

The lack of cameral deposits is unusual in Actinoceratida but typical of Georginidae which are most obviously characterized by siphuncular deposits in which the annulus calcification is in the form of radial lamellae separated by spaces and enclosed within the hollow walls of each annulus (Fig. 3). The calcified radial lamellae and annulus walls are built by growth of fine, small crystals elongated normal to membrane surfaces, both lamellar core membranes and annulus wall membranes. More significantly, Georginidae have an additional series of calcifications engrafted across the outer edges of each interannulus (Figs. 3-5). These structures are here termed *engrafts* as they are inserted into, and incorporated in, adjacent annuli and join them together. The engrafts originate as calcification around longitudinal membraneous ridges on the insides of connecting rings, the engraft core membranes which divide perispatia into longitudinal perispatial sinuses, as distinct from those of normal actinoceratoids. A system of axial and radial canals and segmental sinuses adds to their actinoceratoid resemblences. The lamellar structure is less distinct from the contrasting massive calcification of the normal actinoceratoids than would appear from many actinoceratoid texts. Wade (MS) shows that similar calcification normal to radial lamellar membrane surfaces is characteristic of Actinoceratida in general, although frequently lamellar calcification is of crystals long enough to abut between adjacent lamellae, so that no empty spaces are left between lamellae and recrystallization is facilitated. Teichert and Crick (1974, pl. 2, fig. 3 in particular)



FIG. 4. *Georgina taylori* n. gen., n. sp. approx. × 4. Sagittal section showing canals (axial and radial) and sinuses (segmental).



FIG. 5. Georgina and ersonorum n. gen., n. sp., approx. $\times 2$. White-headed pins: openings of radial canal distributaries. Black-headed pins: openings of segmental sinuses. Upper surface shows an interannulus and views of engrafts.

have figured a normal actinoceratid with similar short lamellar calcification, Huroniella severnense (Foerste and Savage); in this specimen the interlamellar space was partly filled and partly empty. The empty portion they considered a perispatium, equating the annulus wall with the connecting ring, and thus describing the radial lamellae as growing in from the connecting ring (i.e. like engraft core membranes). Small fragments of the actual, very thin, connecting ring are seen in their pl. 3, figs. 2, 5?, where they cover the grooves in the annulus wall that mark the position of the radial lamellae (compare Figs. 3, 5 in this paper). H. severnense has convergently short lamellar calcification, but is otherwise as distinct from the much older Georginidae as any other Actinoceratida. Teichert and Crick (1974) gave a short review of literature in which radial lamellae have been described in the past. These are much less numerous than papers in which they have been figured. Similar structures have been observed in other Actinoceratida including Nybyoceras multicubiculatum Teichert and Glenister (1953, p. 203), Wutinoceras logani Flower and W. lobiferum

Flower (1968) and numerous other authors' illustrations. The radial membranes are much stronger in the Georginidae than in *Armenoceras* from the same beds, but no stronger than those in a superb *Kochoceras tyrelli* from Red River limestone, Garson Mine, near Winnipeg, Manitoba, loaned by Flower. This shows radial lamellae of rather chalky calcite on each side of lamellar core membranes, separated from neighbouring lamellae by clear, crystalline calcite.

The septal necks of the two most common Coolibah Fm. species are extremely varied; their range is from suborthochoanitic to recumbent cyrtochoanitic. By Nora Fm. time the shape of the neck was stabilized early in individual growth in every species.

The simplest form of siphuncle calcification displayed by Georginidae is illustrated in Fig. 5, G. andersonorum. Only young growth stages are suborthochoanitic, later stages in the same species become cyrtochoanitic. Certain similar, slightly inflated, young stages are without engrafts and not now assigned. There is little difference between those with very small or no engrafts. The latter could be extremes of variation in G. andersonorum or the young stage of certain adult specimens which have been rolled to cylindrical shape. Nothing is known of their phragmocones except the chamber spacing which can be inferred. There is no trace of septal necks nor connecting rings, so not even the possession of perispatial sinuses is provable. Their radial canals lie in interannuli which are flat to slightly convex, and, taken in conjunction with the axial space, growth lines and general proportions, make up a generally georginid plan. The stratigraphically oldest individual is a small specimen of this kind from the lowest Coolibah nautiloid fauna at L256, 1/3 of the thickness above the base. It seems possible that this is a poorly known relict ancestral form that may be more sensibly described later under its own familial name, so no attempt is made to define the family Georginidae broadly enough to include these specimens.

The Georginidae are distinguished from all previously described actinoceratoid families by the possession of engrafts. These include both *engraft core membranes* which grow in from the connecting rings and divided each perispatium into a series of longitudinal perispatial sinuses, and *engraft calcification* of fibrous crystals which added many growth lines during their increase in length, finally ceasing growth when the developing annuli engrafted them into their outer edges across the interannuli. The differences between the sets of associated structures in georginid and other actinoceratid siphuncles are

ERRATUM

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Page 7, Column 1, 17 lines from bottom should read: connecting rings, and is incorporated in the outer

so basic as to suggest that they pre-dated calcification of both groups of siphuncles. Another major difference is that georginids appear to have totally lacked cameral deposits while other actinoceratids normally possessed them adapically. This also suggests early separation of normal Actinoceratida and Georginidae. On the other hand the resemblances are even more far-reaching when all nautiloids are considered.

Species are differentiated largely on the shapes (or ranges of shapes) of septal necks and annuli, the approximate position of the neck within a septum (as indicated by the angle between neck and axis) and differences of proportion. A genetic level of diversity is recognized for a rather late species which is divergent from all others in having reduced annuli and a series of irregular endocones which constrict the functional size of the axial cavity to the approximate proportions of the cavity enclosed by the annuli of the other species. Accordingly, the strongly lamellar actinoceratoids with engrafts are here classified as family Georginidae, genera *Georgina, Mesaktoceras.*

Family Georginidae n. fam. Figs. 3–7

TYPE GENUS: Georgina n. gen.

DIAGNOSIS: Fragile, longiconic orthocones with suborthochoanitic to recumbent cyrtochoanitic septal necks, sometimes with a strong contact layer; connecting rings thin, inflated. Siphuncular calcification of vertical radial lamellae within a hollow ring formed by the annulus walls, both lamellae and walls consisting of minute, elongate, calcareous crystals normal to radial membranes and to the insides of annulus wall membranes, and also a series of massive engrafts which radiate inward from longitudinal puckers of the insides of the connecting rings thin, inflated. Siphuncular calcifiedges of the annules, bridging the interannulus and diverting some to most of the radial canals. Radial canals usually break into distributaries inward from the engrafts. Canal distributaries may occur even when the engrafts are few. The radial canal system occupies the radially fluted interannuli which can be generally flat to arched, or produced anteriorly around the centre. The radial canals are consequently straight to sloped posteriad and often show some dendroid branching. Where known, the perispatia consist of a series of longitudinal, stripshaped perispatial sinuses. These are in a position to have received the distributaries of the axial canals; in addition they sometimes can be seen to connect to the axial cavities through passages (segmental sinuses) which open on the annulus surface both before and after the septal necks. More than one axial canal is usual. The axial space enclosed by the siphuncle calcification is more or less dorsal and usually considerably larger than the axial canals. Often sloping neck-furrows indicate sub-ventral siphuncles.

REMARKS: The variety of septal necks in the earlier Georginidae indicates a pool of genetic variation which was quickly lost. The perispatial sinuses are functionally like the open perispatia of other Actinoceratida and could have been derived from, or simplified into, such an open structure. The engrafts are a newly described structure, and one that gave permanency to the system of perispatial sinuses, though in forms where the engrafts are short there is no proof that perispatial sinuses did not communicate laterally at anterior and posterior. The annular calcification, coupled with axial canals, restriction of radial canals to an interannular position, perispatial sinuses within a thin connecting ring, and apparent sinuses forming return passages to the central cavity, are decidedly actinoceratoid in plan. They, and the cyrtochoanitic necks, deny the similarity of crosssections of Georginidae and Intejocerida which have radial vertical plates continuous from segment to segment, allowing a dispersed circulatory system, without perispatia.

Genus Georgina n. gen.

TYPE SPECIES: Georgina taylori n. sp.

DIAGNOSIS: Moderate-sized to large orthocones (known from siphuncles, adjacent fragments of septa, and portions of two phragmocones). Siphuncles probably all more or less sub-ventral. Necks apparently suborthochoanitic in early stages of one species, otherwise moderately cyrtochoanitic (and frequently becoming more cyrtochoanitic during ontogeny) to recumbent. Segments higher than wide to over 5 times wider than high, proportions change markedly during ontogeny of earlier species as length does not increase as much as width, and may decrease; non-adnate to adnate. Engrafts may be few and large to many and regular, varying in and between individuals. The number of radial lamellae calcified is also extremely variable. Interannuli often anteriorly convex near the centre in late stages of growth. Without appreciable extraannular calcareous deposits in the axial cavity.

REMARKS: The canal and sinus system is illustrated by a diagram of the type species in longitudinal section (Fig. 4). In forms with strongly recurved necks the sinuses may lead within radial lamellae (Plate 4, fig. 3), rather than across the interannulus (Plate 4, fig. 7).

Georgina andersonorum n. sp. Figs. 5, 6d–f; Plate 1, figs. 1–4, Plate 2, figs. 1–6

MATERIAL: 16 partial siphuncle fillings ranging from few to 17 segments long. All are from the upper third of the Coolibah Fm.

HOLOTYPE: F7159, from near the top of the Coolibah Fm. in the vicinity of Halfway Dam, Tobermory Station, Northern Territory. This specimen shows the full range of development of the septal necks. It was not broken or badly eroded but it has an aberrantly small amount of calcification in the last annulus.

DIAGNOSIS: Siphuncular segments large, nonadnate throughout or until strongly cyrtochoanitic necks are formed; septal necks suborthochoanitic in young stages or throughout but can quickly change to cyrtochoanitic during ontogeny; engrafts sparse to close-packed; radial canals straight to posteriorly sloped depending on whether the interannulus is near flat or anteriorly convex. Early growth lines in lamellae and anterior growth stages show that annulus calcification is at first concentrated adapically, but usually becomes symmetric about the neck.

DESCRIPTION: The species is large, only slightly smaller than *G. taylori*. It includes specimens with great individual variability in the curvature of the septal necks (Plate 2, figs. 1–3). While only large diameter specimens have strongly cyrtochoanitic late chambers, and at the last the character is introduced rapidly, some of the longest have not reached this stage at all (Figs. 6d–f; Plate 1, fig. 4). Whether every adult in the species would have reached it is uncertain but the trend to sharper inter-segmental constriction is generally present.

The anterior cavity usually grades in through a number of segments but in the holotype at least one third of the diameter of the interannulus is exposed about the centre of the last half-annulus so that radial canal furrows show in the interannulus. At one side the upper half-annulus is broken away and the whole length of the furrows is seen. Study of this area shows that the engrafts also were atypically developed in this area and confined below the interannulus. Concentration of the early calcification below the septum during growth of the annuli is common in the species.

Where engrafts are broad, the sinus openings appear more numerous than one pair each side of the engraft core at the tips of each calcification (Plate 2, figs. 1, 3).

REMARKS: Comparisons of this species with *G. taylori* and *G. beuteli* are found under those species.

The species is named after the Anderson family, owners of Tobermory Station, whose many kindnesses greatly assisted field work.

Georgina taylori n. sp.

Figs. 3, 4, 6h–p; Plate 2, fig. 7; Plate 3, figs. 1–6; Plate 4, fig. 1

MATERIAL: About 70 partial siphuncle fillings ranging from 1-18 segments in length, and to $4\cdot42$ cm in maximum known width. All are from the upper third of the Coolibah Fm. This level is much richer on the SW. limb of the syncline than the NE. but usually concealed in both areas.

HOLOTYPE: F7148, from near the top of Coolibah Fm. in the vicinity of Halfway Dam, Tobermory Station.

DIAGNOSIS: Large, relatively long-chambered shells (dimensions of phragmocone unknown, length of calcified siphuncle estimated to have reached about 50 cm). Septal necks mildly cyrtochoanitic in small diameter specimens, to recumbent in larger individuals. Segments initially globular, height may increase in the early stages but tends to decrease throughout life; width increases steadily (except in some large specimens where it may slightly diminish over the last few chambers). Early segments almost normal to axis but later, wider segments tend to become oblique. Contact layer forms a platform in the intersegmental constriction. In addition to radial canals (presumably arterial) a series of openings at the upper and lower ends of engrafts lead into sinuses in the interannulus or oblique canals within lamellae in larger specimens. (These seem to have been a venous system running inward from the perispatial sinuses into which radial canal distributaries appear to have opened.)

DESCRIPTION: The remaining shell fragments permit the observations that the septa were extremely thin for the chamber height, and that there is no evidence of cameral deposits. The septal necks are sometimes thickened relative to the septa, particularly if they are recumbent. The necks are fully lined by connecting ring material; this is so at all stages of growth. The neck linings form strongly calcified contact layers. On lightly etched specimens these form platforms with edges standing above the adjacent siphuncular beads, when the necks are dissolved away. A two-layer effect may be seen which comprises the contact layer and a darker layer like the remainder of the connecting ring in texture, presumably a layer containing more organic material in life. The free portions of the rings may have been very lightly calcified as they are rarely preserved and extremely thin for a structure normally calcified by elongate spicular crystals.

The outlines of a number of pieces of different sizes are shown in Fig. 6h-p, to bring out the general growth trends. It is not certain that the initial segment has been observed but the trend in small specimens is toward globular. Most specimens have a slow decrease in segment length but in Fig. 6 o the rate is practically zero. As in most nautiloids the later segments of large specimens are relatively short, and in one (Fig. 6j) the segments of the anterior end are minimally narrower than the lower portion. This narrowing has been observed on 3 or 4 other specimens but all the others are somewhat deformed, as if the incompletely calcified part was slightly plastic during burial.

In transverse sections the axial cavity is seen to be irregular. In longitudinal section, therefore, it rarely runs straight from top to bottom, and may appear to change greatly in size. When preserved, the axial canals take up only a fraction of the space in the cavity (Plate 3, fig. 1d). The angles at which the radial canals diverge from the axial cavity are controlled by the growth of the calcified annuli below and above the interannulus; they tend to lie in some of the fluted depressions that result from the growth form of annuli, and to shape them in detail. The angle at which they diverge from the axial canal itself is usually more oblique than the surface of the interannulus (Fig. 4).

Plate 4, fig. 5 shows a naturally silicified and etched section of a specimen broken through the centre of the septal neck, the point of origin for all radial lamellae. It therefore shows the maximum number of lamellae in this annulus. As inward growth continued the number of lamellae diminished and the fewer, remaining lamellae reached not only further in but further up and down, reaching to the equatorial region where they abut on the engrafts which, having started growth at about the same time, were calcified masses prior to enclosure among the outer ends of the lamellae. The central furrows of the engrafts, seen in most external views, equate with the dark line or core membrane seen as the centre of calcification in sections. In Plate 4, figs. 6, 7 the connection between the connecting ring and the core is shown. It can be found in other places in these and other specimens. The canal distributaries lead to the surface around or between the engrafts. Because the inside of the connecting ring extends inward as the cores of the engrafts (Fig. 4) the perispatium is divided into longitudinal strips (Plate 4, figs. 1, 2; Plate 6, figs. 1-3). At the anterior and posterior tip of each of the engrafts a pair of pores lead into the annulus. They are separated from one another by the cores of the engrafts and (unless the neck is recumbent) lead into sinuses that run between the engrafts and the annulus walls to the interannuli (Fig. 4; Plate 4, fig. 7). They are often separated from the nearest distributary and radial canals by so little space that in section, unless both are present, it is not always possible to tell whether canals or sinuses are the structures in view. Oblique canals seen in recumbent-necked portions of large specimens (Plate 4, fig. 3) reach the surface at a spot coincident with these pores and appear to be an alternative development of the sinuses. In most specimens the ring of pores also marks the edge of the contact layer platform area, but in many specimens with recumbent septal necks the contact layer platform forms a shelf overhanging the pores without blocking them.

REMARKS: The closest species are *G. anderso*norum and *G. beuteli*. *G. andersonorum* as at present known is slightly smaller; it is nearly the same in the structures of its lamellae though early growth is concentrated below the neck; engrafts and canals are similar; it differs in being non-adnate until a very late stage of growth, and only slightly so, at most. It lacks a contact layer platform. Its early segments, or even most of its segments, are connected by wide, gently curved constrictions which most probably housed suborthochoanitic septal necks, a degree less curved than any *G. taylori*. *G. beuteli* is compared after its description.

In two most extreme large individuals the pattern of surface structures is modified to such an extent that these specimens can only doubtfully be assigned to *G. taylori*.

The species is named after Mr D. J. Taylor who first drew my attention to the locality and fauna.

Georgina beuteli n. sp. Figs. 6a-c; Plate 5, figs. 6, 7

MATERIAL: Three specimens are known from the upper third of the Coolibah Fm., Tobermory, and one from the top of the formation at Glenormiston.

HOLOTYPE: F7219, from the upper third of the Coolibah Fm. near Halfway Dam, Tobermory.

DIAGNOSIS: Moderate size with high chambers. A very smoothly streamlined profile to the beaded siphuncle is produced by smoothly rounded segments and moderately cyrtochoanitic necks with a thin contact layer that does not form a platform. Engrafts usually slender, some groups of them are longitudinally arcuate. Radial canals are relatively straight and their distributaries form a nearvertical fan. DESCRIPTION: The holotype is the only relatively large specimen. Segment height as well as width increases throughout this six-segment piece (Fig. 6c; Plate 5, fig. 6). The contact layer still adheres in most of the constrictions but is too thin to form a platform. Segments are not oblique to the axis. Little more can be added to the diagnosis. The packing of the canal distributaries into near vertical planes is a consequence of the narrow engrafts rather than an independant character; it is a noticeable feature in vertical sections.

REMARKS: G. beuteli is distinguished from G. taylori by its very regular proportions, having mildly cyrtochoanitic necks and smoothly inflated chambers throughout its known length, unobtrusive contact layers, and slender engrafts which are not necessarily straight but can be arcuate in a longitudinal direction. It resembles G. dwyeri from the middle of the overlying Nora Fm. in segment shape, though it is very sharply differentiated from G. dwyeri by the fact its segments are not obliquely set, and contact layers are symmetrical. Its engrafts are also less frequently arcuate. Although G. andersonorum also lacks an obvious contact layer its necks vary abruptly from much less curved than those of G. beuteli to much more curved, and it virtually omits the shape of neck and segment which characterizes G. beuteli.

The species is named after Mr E. Beutel of the Queensland Museum, who rendered outstanding service during the 1972 trip.

Georgina linda n. sp. Fig. 6g; Plate 5, figs. 1–5, 8

MATERIAL: Two specimens from 3 km SE. of Linda Creek, Glenormiston Station, L251, in a limestone lens in the sandy lower beds of Nora Fm. Fragmentary specimens from the lower part of Nora Fm. at L319, Toomba Range.

HOLOTYPE: F7176, Glenormiston (L251).

DIAGNOSIS: Moderate-sized compact siphuncles, segments over twice as wide as long, with recumbent necks throughout (No other portion of phragmocone preserved). Axial region occupied by several parallel canals which give off 'straight' radial canals with longitudinal fans of distributaries. Engrafts narrow and usually wavy longitudinally.

DESCRIPTION: The holotype gradually increases in height and width of segments from its first to its fifth segment, and diminishes even more slightly over the sixth and seventh segments, the shorter topotype is of 3 slightly larger segments. The specimens from L319 have deeply etched surfaces and most are single segments; some appear to have been less tightly recumbent than those from L251, but they are closely similar. The neck openings are little more than half the width of the segments at their equators (Fig. 6g). The segments are slightly oblique, the more adnate side being slightly advanced, so the siphuncles must have been slightly off-centre in the phragmocone. Free portions of connecting rings are absent but the ends of the perispatial sinuses are present between the intrasiphuncular deposits and the adnate portions of the connecting rings. A bundle of parallel axial canals is preserved in the holotype. Radial canals straight, branching in the outer portions of the interannuli, distributaries tend to form longitudinally spread fans between engrafts (Plate 5, fig. 3).

REMARKS: In its narrow, wavy engrafts *G. linda* resembles *G. beuteli* and more particularly *G. dwyeri*. It differs from both, however, in its strongly recumbent septal necks. Its slightly oblique intersegmental furrows show that it had a near-central siphuncle, more off-centre than *G. beuteli* and less off-centre than *G. dwyeri*.

Georgina dwyeri n. sp.

Fig. 7a-f; Plate 5, fig. 2, Plate 6, figs. 1–3a–d

'Actinoceratid gen. et sp. nov'. Hill, Playford and Woods, 1969, p. 4, Plate O2, fig. 14.

MATERIAL: All specimens are from the lower upper Nora Fm. at the foot of Toko Range scarp, from Neeyamba Hill, Oodatra Point and 3 km SE. of Poodyea Point (L312). Since many of the specimens have been obtained in scattered fragments that cannot be fitted together, the number of individuals is in doubt. It was no less than thirty. The rock is a silty coquinite and the fossils in it have not been silicified but recrystallized and sometimes internally partly replaced with siderite which has mostly oxidized, obliterating structure; some are partly calcified internally. They tend to crumble with the rock under full exposure to insolation and cooling.

HOLOTYPE: University of Queensland F66033, from 3 km SE. of Poodyea Point, Glenormiston Station.

DIAGNOSIS: Some individuals reached large size (the calcified part of the siphuncle is estimated to have reached over 100 cm); siphuncle segments averaged a slow, rather uniform increase in width and length till a late growth stage. The siphuncle was near ventral as segments were oblique to the axis and less rotund on the advanced side where the posterior adnation area (i.e. posterior end of each segment) was flattened and consistently broad. Moderately cyrtochoanitic septal necks. Chambers long, with fragile septa. Engrafts mostly long and slender, wavy or straight. Axial canals probably multiple, radial canals straight to posteriorly curved, some dendroid branching. Axial cavity rather broad and rounded at all stages of growth. Wavy longitudinal grooves occur on the surface of some large individuals (these may indicate perispatial sinuses).

DESCRIPTION: The size-range is large. Fig. 7a-f shows scale diagrams of specimens ranging from a minimum of 1.9 cm diameter and 1.2 cm long to 4.8 cm wide and 2.4 cm long. The longest specimen (Fig. 7e) consists of just over 27 segments and is 35.4 cm long. The next longest is a much larger individual, 17 segments occupy 33 cm; as Fig. 7a shows, it has relatively short segments for its diameter. The last few segments enclose part of the anterior cavity. If its angle of taper is produced until the width of the smallest specimen figured is reached, the length obtained is approximately 100 cm but even then both ends are missing. The section of the holotype, similarly produced, gives a length of 70 cm but no trace of the anterior cavity occurs in this (Plate 6, fig. 1a-d). One metre is thus a reasonable estimate of the possible length of a calcified siphuncle. The curvature of the septal necks is moderately cyrtochoanitic with a little variation. The segments are consistently oblique, and when the neck linings are preserved they form contact layer platforms with a pronounced broadening toward the anteriorly sloped side of the segment. This portion of the segment is flattened relative to the remainder of the segment outline, from contact with the septum. Restored shell outlines are suggested in Fig. 7b, the basis of restoration being the small, gently up-turned piece of septum showing in Plate 6, figs. 4-6, the contact layer platforms, and the almost unvarying siphuncle outlines. The perispatial sinuses on large specimens may or may not be quite deeply impressed (Plate 6, fig. 2) although small specimens are quite smooth. In addition to these channels, Plate 6, fig. 1, shows fine ridges along the cores of the engrafts, these are apparently the puckers of the inside the connecting ring. Radial canals tend to be straight in smaller specimens and posteriorly curved in larger individuals. The angles at which they meet the central cavity suggest they attached to several axial canals. Strongly oblique passages seen in several specimens have not been traced to their outer limits and may be the inner ends of sinuses which open adjacent to the contact layer platforms like those in Plate 6, figs. 5, 6. A few thin layers of secondary calcification line the apical end of the axial space in some specimens.

REMARKS: This is the only species beside the older *Mesaktoceras arachne* which has any secon-

dary deposit in the axial cavity. It is here a very minor amount which scarcely constricts the axial space, and is not correlated with reduced annular deposits. The mildly cyrtochoanitic necks have a resemblance to *G. beuteli* but this yet older form is decidedly smaller and has segments which do not slope anteriorly on the ventral side, and do lack the skewed adnation area, i.e. its siphuncle was much more centrally placed in the phragmocone.

The species, which has been found only on Glenormiston, is named after the Manager, Mr J. Dwyer, in recognition of his great helpfulness to the field parties, and interest in the work.

Mesaktoceras n. gen.

Type Species: Mesaktoceras arachne n. sp.

DIAGNOSIS: Georginidae with strongly cyrtochoanitic necks; engrafts well developed; radial lamellae very reduced, often not in contact in adjacent annuli and so not enclosing the inner ends of engrafts; a secondary calcareous deposit lines the irregular axial space with matchingly irregular endocones that almost fill its lower parts, enclosing canals and sinuses.

REMARKS: In the development of endocones *Mesaktoceras* has a superficial resemblance to the parietal deposits and endocones of several Discosorida but its primary deposits are the two series, annuli and engrafts, developed in all Georginidae. The canal and sinus systems enclosed by the calcareous deposits are also actinoceratoid, and appear to have been linked by vertical perispatial sinuses.

Mesaktoceras arachne n. sp. Fig. 7g–j; Plate 7, figs. 1–7

MATERIAL: Eight specimens from 1 km east of Halfway Dam, Tobermory, from the middle of the Nora Fm. which is here relatively strongly calcareous. In Toomba Ra. one specimen was collected from a narrow calcareous bed among sandstones approximately at this level, and two from a large calcareous lens in the lower member. On the NE. limb only two small calcareous lenses at L251 occur in sandstone in this span, and only two fragmental specimens were found.

HOLOTYPE: F7187, from 1 km E. of Halfway Dam, L328.

DIAGNOSIS: As for genus.

DESCRIPTION: The largest specimen is 28 segments (approximately 34 cm long); it lacks both ends but not many segments from either end (Fig. 7h), and is distorted by dorsoventral compression. Septal necks are strongly cyrtochoanitic; in small



FIG. 6. Profiles of *Georgina* n. gen., × ¹/₂, outlines obtained by combined measuring and sketching or direct tracing off medial sections, or photographs × 1. (a-c) *G. heuteli* n. sp., c = holotype. (d-f) *G. andersonorum* n. sp., d = holotype. (g) *G. linda* n. sp., holotype. (h-p) *G. taylori* n. sp., o = holotype. The initial chamber may be present on m, its anterior cavity is also present, as on h, i, and the last segment or two of other specimens.



FIG. 7. Georginidae, $\times \frac{1}{2}$, profiles prepared as Fig. 6. (a–f) *Georgina dwyeri* n. gen., n. sp., b=holotype, position of siphuncle restored from adnate ventral and free dorsal edges of septum. (g–j) *Mesaktoceras arachne* n. gen., n. sp., g=holotype, h, dorsal view of longest specimen (flattened dorsoventrally, anterior cavity present but rock-filled).

specimens they have an open loop at the inner end but they become totally recumbent in larger specimens (Figs. 7i, j). The overall shape of segments changes very gradually and regularly as widening outstrips height. Contact layers are thin. The connecting rings are separated from the siphuncle calcification by a narrow gap which is now only rarely bridged by thin ridges at the cores of engrafts. This evidence is sufficient to justify the assumption that the perispatium was at least partly divided into vertical sinuses but, as in some other species, the engrafts do not always reach from septal neck to septal neck, and there is no evidence at all of whether perispatial sinuses were always complete, or fused laterally if the engraft was short.

Horizontal sections near the interannulus show only engrafts and endocones but other sections also show radial lamellae. Their size is restricted, particularly on the dorsal side (Plate 7, fig. 4). The ventral side is indicated by the anterior slope of segments as well as greater overall calcification. No canal walls are preserved but growth lines in the calcareous deposits were strongly deflected outward and appear to have encased slightly curved canals in the interannuali (Plate 7, figs. 4–6); they are usually less strongly deflected around wider spaces in the position of the sinuses (Plate 7, figs. 4, 5). It is not always possible to prove whether a particular space in an intermediate position was a canal or a sinus.

REMARKS: The classic cob-web shape of the endocones in transverse section makes even isolated segments of *M. arachne* distinct from the other known Georginidae. It is also unique in having strongly reduced radial lamellae (i.e. reduced annuli). Like G. linda and G. dwyeri, M. arachne is differentiated from the earlier G. taylori and G. andersonorum by much more regular shape. The slight change of its septal necks, from recumbent with an open loop at the inner end to tightly recumbent, is perceptible only in section. Although the late chambers of M. arachne and G. taylori are often similar in shape, the early to medium sizes are glaringly dissimilar (Figs. 6h-p, 7g-j). G. linda also is higher in proportion to width than *M. arachne*, and tightly recumbent throughout (Fig. 6g). Other named Georginidae are not recumbent.

CONCLUSIONS

The distinctiveness of Georginidae from other Actinoceratida does not rest only upon the so obvious differences in calcification which, except for the engrafts, are more a difference of degree than basic structure (Wade, MS). Cameral deposits, common in Actinoceratida, appear to have been lacking in Georginidae. The perispatial sinuses of Georginidae do not allow secondary deposits such as have been recognized in other Actinoceratida.

One species stands apart because it alone has diminished annulus development, and it has strongly developed endocones lining its otherwise large and irregular axial cavity. Only a minute amount of secondary material lines the base of the axial cavity in any other species. This association of two well-developed independent trends has been used to separate a monotypic genus Mesaktoceras from the remainder, genus Georgina. The Georginidae were successful enough to reach a large size in this shallow epicontinental sea, but their extreme fragility must have weighed against them as their size, and that of less fragile competitors, increased. The last known form, G. dwyeri, is the largest. Although the Georginidae at present have been found only in carbonate facies, and carbonate lessens toward the top of the Nora Fm., G. dwyeri ceases at a level within sandy, silty coquinites. The observed cut-out thus may be actual, and the group not succeed Lower Middle Ordovician.

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Scales in mm.

- FIGS. 1–4. *Georgina andersonorum* n. gen., n. sp., F7135, paratype, siphuncle filling only, Halfway Dam, Tobermory. 1, ×2, Section through calcified material (between pointers on fig. 4) confirms shape of silicified, weathered surface and shows matrix between calcareous radial lamellae. 2–4, ×1. Dorsal and anterior lateral views showing increasing relative and absolute size of engrafts and steepening curvature of septal constrictions. Broken section at right shows the lamellar annuli, interannuli, and engrafts.
- FIG. 5: *Georgina* sp., CPC16908, $\times 1$. Specimen with most shell preserved. Oblique horizontal section showing a relatively small siphuncle and correspondingly low chambers.



Scales in mm.

FIGS. 1-6: Georgina andersonorum n. gen., n. sp. 1-4, F7159, holotype, \times 1, Halfway Dam, Tobermory. 1–3 show an abrupt transition from broadly curved to furrowed septal constrictions and predominately large, widely-spaced engrafts. 1 also shows pores (at level of pointer) that are not associated with engrafts, as well as those that are; both lead into segmental sinuses, while radial canal distributaries are nearer the bulge of the segments. 4, anterior end, shows an aberrant last half-annulus which is also broken so that the full length of radial canal furrows is exposed in the interannulus at lower right. 5, 6. F7164, paratype, 5 km. N.W. of Halfway Dam, Tobermory, ×2. 5 shows 2 connecting rings and adjacent septal necks. Anterior neck bears a partly developed annulus with light grey early layers restricted to coating the posterior (free) edge. 6, posterior to 5 and opposite side of saw-cut. Anterior two segments show radial canals with one distributary each, a narrow perispatium is preserved in the anterior segment but no connecting rings are preserved in the posterior two. Segmental sinus openings occur above and below engrafts, and the Yshaped traces of the interannular wall membranes separate engrafts from annulae.

FIG. 7: G. taylori n. gen., n. sp., F7134, paratype, $\times 2$. Anterior cavity in transverse section a short distance from an interannulus. Engrafts are contiguous almost all around the circumference, and are enclosed on their inner sides by blister-like sectors which together make up the part-developed annulus. Predepositional erosion has left an unnaturally rough surface.

PLATE 2



Scales in mm.

FIGS. 1—6: Georgina taylori n. gen., n. sp., ×1, Halfway Dam, Tobermory. All show the contact layer platform covering the annulus in their septal constrictions. Sometimes the septum is adherent to it, and the broken edges of septa can be seen in fig. 6, partly peeled from the contact layer platforms in the posterior septal constrictions of fig. 6. 1–4, F7148, holotype. The pointer on fig. 4 indicates the broken end of a silicified tube (axial canal) in the axial cavity. 5, F7101, paratype, young individual; weathering cracks slightly expanded its posterior end. 6, F7139, paratype, large, well-preserved specimen.



PLATE 4

Scales in mm.

FIGS. 1–7: Georgina taylori n. gen., n. sp., paratypes. 1, 2, × 1.5 F7111. 1, longitudinal and oblique transverse sections; pointer at side indicates an engraft sectioned approximately through its dark 'core membrane'. The interannular membranes are occasionally bulged apart by canals. The top indicator, like those in fig. 2, points out the organic walls of the perispatial sinuses between the annulus and (fig. 2) the connecting ring. Only the tips of some engrafts are seen in transverse sections because the section is close to the septum. 3, F7121, partial longitudinal section of large individual showing transverse canal through annulus. 4, F7130, transverse section near septal constriction of specimen with extreme development of radial lamellae. 5, F7091, naturally etched specimen broken through septal neck, radial lamellae most numerous outwardly, axial space irregular, externally the annulus interdigitates with the engrafts, and engraft core membranes are represented by furrows. 6, F7106, ×2, near tangential section through engraft showing core membrane attached to connecting ring, 7, F7149, $\times 2$, longitudinal section passes from one side to the other of the engraft core membrane (inner edge of core membrane at white pointer), a perispatial sinus makes a thin dark line outside the whitish calcite laid on the far side of the core membrane; connecting ring dark, core membrane merges with ring between dark pointers; a second perispatial sinus leads into a passage (segmental sinus) leading inward across the anterior tip of the engraft into the interannulus. The naturally strongly recurved septal neck appears recumbent because the septum was forced down by a lump of detritus.



Figs. 1-8, scales in mm. Fig. 9, scale in cm.

- FIGS. 1–5, 8: Georgina linda n. gen., n. sp., 1–3, F7176, holotype, 3 km
 SE. of Linda Ck. and 5 miles NE. of 26 bore, Glenormiston. 1, 2, × 1 oval effect accentuated or induced by wear. 3, ×1·5, longitudinal section showing several axial canals, radial canals, and (lower right) a fan of canal distributaries. 4, ×1, F7177, paratype, locality as above, external view of less worn specimen. 5, 7185, ×1, and 8, F7178, ×1·5, L 319, Toomba Range, paratype transverse sections near interannulus, showing outer ring of engrafts and radial lamellae encircling (5) the base of the anterior cavity and (8) the axial cavity.
- FIGS. 6, 7: Georgina beuteli n. gen., n. sp., $\times 1$, Halfway Dam. Tobermory. 6, F7219, holotype; traces of very thin contact layers adhere in some of the septal constrictions, and the engrafts are very narrow as in 7, F7220, paratype, (right side truncated by penecontemporaneous erosion).
- FIG. 9: Georgina dwyeri n. gen., n. sp. $\times \frac{1}{2}$ (scale in cm.), paratype, U.Q. F60014, venter to right.



Scales in mm.

FIGS. 1-6: Georgina dwyeri n. gen., n. sp. 1, F7206 paratype, × 2, external view of siphuncle filling showing edges of contact layer platforms, narrow, curved engrafts with core membranes preserved as dark, organic-rich, calcite (c/m), and rock-filled furrows (perispatial sinuses) between the engrafts. Burrows cause shadows at lower right. 2, U.Q. F67153, \times 1, paratype, furrows or perispatial sinuses crossing the segment were previously covered by connecting ring. 3-6, U.Q. F66033, ×1, holotype. 3, dorsal view, shows engrafts with core membranes at pointers, and perispatial sinuses between them. 4, lateral view, slightly worn, fragment of septum with neck at pointer. 5, 6, dorso-ventral longitudinal section, dorsal sides adjacent, whitish shell fragment with septal neck lined by dark contact layer at pointers. Similar contact layers coat all the septal constrictions and the pronounced ventral adnation areas. Radial canals occupy the interannulus at the top right 2 segments of fig. 6, and partly occupy the 3rd and 4th interannuli on the left of fig. 5, and its bottom right interannulus. Segmental sinuses can be traced from their external openings at the anterior and posterior of engrafts to the interannulus in the three upper left segments of fig. 6 and the left next to top segment of fig. 5. Axial cavity typically large and straight.



Figs. 1-6, scales in mm. Fig. 7, scale in cm.

FIGS. 1–7: *Mesaktoceras arachne* n. gen., n. sp., 3 km. E. of Halfway Dam, Tobermory. 1–3, F7187, holotype (includes 6 additional posterior segments), 1, 2, \times 1, 3, \times 2. White stipple in the centre of 3 covers the rock fill of the axial cavity, section through interannulus shows only engrafts and endocones. 4, F7188, paratype, \times 1, longitudinal section, dorsal to left, ventral, right. Annuli reduced on dorsal side relative to ventral, so that engrafts are larger on dorsal. Endocones extend through 6 or more segments. Probably segmental sinus at S. radial canals at r. 5, F7193 paratype, \times 1.5, vertical section showing fully developed axial cavity. 7, F7189, paratype \times 0.6, longest specimen, flattened in the plane of the paper, incomplete at both ends but with lower part of anterior cavity present.



